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How does grazing management influence the functional diversity of oak woodland ecosystems? A plant trait approach.

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Abstract

Traditional approaches to conservation often focus on plant species composition. In contrast, trait-based approaches highlight the role plant species play in ecosystem function, with a focus on functional diversity and its importance for ecosystem resilience. Here we utilise a plant-trait approach to explore the association between livestock grazing intensity and plant functional diversity in Atlantic oak woodlands, a conservation priority habitat. In two historically un-grazed woodlands (subject to periods of light sheep grazing in winter) paired with two grazed woodlands (intensively grazed by sheep or feral goats), in north-west Wales, UK, field plant-trait data were recorded in three (30 x 4 m) plots per woodland for trees, saplings and understory plants. For trees and saplings, plant-trait data from the field (specific leaf area (SLA) and leaf dry matter content (LDMC)) were combined with plant tolerance indices from the scientific literature (shade, drought and water-logging tolerance) and used to calculate community weighted means (CWM) and functional diversity for plot-level communities. Three plant traits (LDMC, mean foliage height and growth form) and two Ellenberg indices (light and moisture) were combined to calculate CWM and functional diversity for understory plant communities. Tree and sapling communities from grazed

woodlands were characterised by response traits associated with grazing avoidance strategies (high LDMC, low SLA), and higher shade- and drought-tolerance scores but lower water-logging-tolerance scores than in un-grazed woodlands. Tree and sapling communities in the un-grazed woodlands had greater seedling establishment, sapling recruitment and functional diversity than in the grazed woodlands. Plant-trait values and functional diversity did not differ with grazing intensity for understory plants. Land managers are increasingly being asked to manage semi-natural habitats for 'resilience to future events' such as droughts or floods. Here we demonstrate how a plant-trait approach, including assessment of community-level tolerance indices, allows us to infer potential associations between grazing management, functional diversity and ecosystem resilience.

Keywords:

Atlantic oak woodlands, Ecosystem resilience, Forest pasture, Herbivory, Stress tolerance, Wood pasture.

1. Introduction

Atlantic oak woodlands are a priority ecosystem for conservation within Europe (European Commission, 2015), characterised by high rainfall, base-poor soils and biodiverse bryophyte communities. Despite their high conservation importance many are listed as having unfavourable conservation status, threatened by fragmentation, inappropriate grazing management and invasive species (JNCC, 2013). Traditional approaches to woodland conservation focus on plant community composition and diversity (Hansson, 2001; McEvoy et al., 2006) and sapling recruitment (Palmer et al., 2004), with poor regeneration of oak

(*Quercus* spp.) of particular concern (Shaw, 1968a; 1968b). More recently, trait-based approaches to plant community ecology have been advocated, as a basis for conservation management, in a range of terrestrial ecosystems (Cadotte, 2011) including forests (Andersen et al., 2012; Craven et al., 2016; Mokany et al., 2015). These trait-based approaches highlight the role plant species play in ecosystem function, exploring the emerging relationship between functional diversity and resilience to future perturbations (Standish et al., 2014). Here we define *resilience* as the degree to which ecosystem function can resist or recover rapidly from environmental perturbations (Oliver et al. 2015) as mediated by plant functional traits.

Plant functional traits can be defined in two broad ways: i) as any measurable characteristics at the individual level that directly or indirectly affect plant fitness (Lavorel et al., 1997; Violle et al., 2007); or ii) characteristics of individuals or species that influence ecosystem-level properties and processes (Petchey and Gaston, 2006). Plant traits are commonly categorised as either: i) *response traits* – traits associated with an individual or species response to environmental change such as grazing, drought or flooding; or ii) *effect traits* – traits that determine the effect of plants on ecosystem functions such as nutrient or biogeochemical cycling (Lavorel and Garnier, 2002). A greater functional diversity (i.e. variation in functional traits within a community) of effect traits is expected to result in enhanced community-level plant productivity and resource-use efficiency (Díaz et al., 2001). For response traits, greater functional diversity can enhance a community's resilience to a range of environmental disturbances (Díaz et al., 2001; Elmqvist et al., 2003; Loreau et al., 2001; Standish et al., 2014), such as grazing by large herbivores, flooding or drought, by providing a higher response diversity.

68 The impact of livestock grazing on community-level plant traits has been summarised by
69 several classic plant-resource models: Grime's (1977) CSR (Competitor, Stress-tolerator,
70 Ruderal) model, Coley et al.'s (1985) resource availability model and Westoby's (1998) LHS
71 (leaf-height-seed) model. These models predict that: i) selective or low-intensity grazing
72 favours unpalatable plants with low specific leaf area (SLA) (Cornelissen et al., 1999;
73 Coughenour, 1985) and higher leaf dry matter content (LDMC) (grazing avoidance); and ii)
74 intensive non-selective grazing favours short, often palatable, plants with high SLA indicating
75 fast regrowth of high-quality tissue with low structural defence (grazing tolerance),
76 particularly in humid or productive grassland systems (Díaz et al., 2001). This framework,
77 particularly relevant in woodlands to understory plant species, may also be affected by
78 canopy openness with more open woodlands characterised by fast-growing understory
79 species with traits indicative of grazing tolerance strategies such as high SLA (Brocque et al.,
80 2009). For sapling communities, grazing avoidance strategies may be favoured, with low SLA
81 and high LDMC effective at deterring herbivory (Westoby et al. 2002) as these traits tend to
82 be coupled with the allocation of more tannins, phenols or other defensive compounds to
83 leaves (Coley, 1983). Indeed, under open-canopy and intensive livestock-grazing conditions,
84 sapling SLA was found to be lower than in un-grazed forests (Carlucci et al., 2012).

85 In addition to commonly studied response traits such as SLA and LDMC, traits linked to plant
86 response to variation in the physical environment, e.g. tolerance of shade, drought and water-
87 logging, have recently been incorporated into studies evaluating the impact of land-use
88 intensity on functional diversity and ecosystem resilience (Carreño-Rocabado et al., 2012;
89 Carreño-Rocabado et al., 2016; Craven et al., 2016). Some studies have focused on how
90 grazing interacts with response plant-traits related to the physical environment, especially
91 drought tolerance (Deléglise et al., 2015, Leiva et al., 2013; Plieninger et al., 2011; Tucker et

al., 2011). In a further advance, Niinemets and Valladares (2006) developed proxies for environmental response plant-traits based primarily on Ellenberg indices of shade, drought and water-logging tolerance which they extrapolated to over 800 species of trees and shrubs from the northern hemisphere, in lieu of trait-specific information.

The effect of grazing on plant functional diversity has been discussed through the lens of 'environmental filtering' where strong abiotic or biotic filtering effects (e.g. heavy grazing pressure) are expected to select for convergent trait values for co-occurring species, leading to a loss of functional diversity (Ackerly and Cornwell, 2007; Cavendar-Bares et al., 2004; Kraft et al., 2008). Most studies on the impact of livestock grazing on functional diversity in woodland ecosystems have focused on the understory plant community, finding that an increase in grazing intensity leads to either increased (Mandle & Ticktin, 2015) or decreased (de Bello et al., 2006) functional diversity. Results from studies of the response of grassland functional diversity to livestock grazing are also inconsistent, with grazing either reducing plant functional diversity by favouring a limited set of trait values related to either avoidance or tolerance strategies (Catorci et al., 2014) or enhancing it, when compared to un-grazed grasslands where tall grasses dominate (Komac et al., 2015; Vandewalle et al., 2014).

In this study we utilised a plant-trait approach to explore the association between livestock grazing and plant community response traits, tolerance indices and functional diversity in oak woodlands. We expected: 1) in the understory plant community of grazed woodlands response trait values associated with grazing tolerance strategies (low LDMC, low mean foliage height) to dominate; 2) in the tree and sapling communities of grazed woodlands response traits linked to grazing avoidance strategies (e.g. low SLA, high LDMC) to dominate; 3) in the tree and sapling communities of both grazed and un-grazed woodlands trait values

115 associated with shade and water-logging tolerance scores to be greater than those associated
116 with drought tolerance due to the high year-round rainfall in the study area; 4) in the un-
117 grazed woodland plant communities functional diversity to be greater due to the effect of
118 environmental filtering on the grazed woodlands.

119

120 **2. Methods**

121 *2.1 Study area and sampling design*

122 Two pairs of Atlantic oak woodlands, identified as upland oakwood, a priority habitat for
123 conservation and designated as Site(s) of Special Scientific Interest (SSSI), were selected in
124 north-west Wales, UK. One pair is in the area of Ceunant Llennyrch and the other 15 km away
125 in Nant Gwynant (Table 1).These woodlands are managed by the government conservation
126 agency Natural Resources Wales (NRW), alongside two non-governmental organisations: the
127 Woodland Trust (at Ceunant Llennyrch) and the National Trust (at Nant Gwynant). These
128 woodlands are remnants of natural woodland that originally covered most of the Atlantic
129 fringe of Europe, influenced by the Gulf Stream to create the warm, wet microclimate of a
130 temperate rainforest with > 200 days per year of precipitation ≥ 1 mm (JNCC, 2013). Annual
131 precipitation is ~3400 mm with mean, maximum and minimum temperatures of ~10, 19 and
132 -1.5 C respectively (Robinson et al. 2017). These woodlands are dominated by *Quercus*
133 *petraea*, with lower abundance of *Betula pubescens*, *Corylus avellana*, *Fraxinus excelsior*,
134 *Sorbus aucuparia* and *Ilex aquifolium*. Within each of the two study areas, one woodland was
135 selected that had a known history of intensive grazing (managed sheep or feral goat) for at
136 least the past 25 years, and the other managed with no or only light winter grazing over the
137 same time period due to fencing to exclude the animals (Table 1). Sheep and feral goats were

138 the only large mammal herbivores in the study area over this period with cattle and deer
139 absent [Local Environmental Records Centres Wales, http://www.lercwales.org.uk/]. For
140 Ceunant Llennyrch the paired woodlands were adjacent to each other, with the intensively
141 grazed woodland close to sheep grazed pasture-grassland. For Nant Gwynant the selected
142 woodlands were on opposite sides of the valley, 1 km apart, separated by a road and a lake
143 (Llyn Dinas) but both of similar elevation and adjacent to heathland habitat. Soils were
144 classified for both sets of paired woodlands as freely draining acid loamy soils on rock using
145 Soilscapes, a 1:250,000-scale, simplified soils map covering England and Wales developed by
146 the LandIS [Land Information System) team, Cranfield University, http://www.landis.org.uk/].

147 After a preliminary survey to assess the conditions typical of each woodland (i.e. species
148 composition and relative abundance of trees, saplings and understory plants, and slope
149 angle), three 30 m x 4 m plots were established within each of the four study woodlands to
150 represent these conditions. Plots were positioned ≥ 10 m away from woodland edges with
151 large rocky outcrops excluded. All plots included *Q. petraea* and other tree species
152 representative of each woodland. In addition, three 1 m x 1 m sub-plots were established,
153 equally spaced along the length of each plot, for assessment of environmental and understory
154 characteristics including seedling establishment (Appendix, Fig. A1).

155 *2.2 Environmental characterisation*

156 Total basal area (m^2 ha^{-1}) and stems per hectare (ha^{-1}) of trees and saplings were calculated
157 from the mean of plot-level measurements and scaled up. Seedling density (m^{-2}) was
158 calculated from 1 m x 1 m sub-plots. Soil temperature, moisture, pH and bulk density were
159 recorded in each sub-plot. Soil temperature was measured across the top 10 cm of soil with
160 a Checktemp thermometer (Hanna Instruments). Soil pH was measured in water according to

161 Smith and Doran (1996) in a 1:2.5 v/v slurry. Soil bulk density in the top 5 cm of soil was
162 measured using a stainless steel ring (5 cm height, 5 cm diameter). Gravimetric soil moisture
163 content (%) was also calculated from each bulk density soil sample. All environmental
164 characteristics were measured during July 2016; on four days within a 14 day window,
165 avoiding days with precipitation ≥ 3 mm.

166 *2.3 Plants traits*

167 All plant trait data were collected in July 2016, in tandem with the environmental sampling.
168 Within each plot all trees (≥ 10 cm diameter at breast height (1.3 m, DBH) and saplings (<10
169 cm DBH but > 1.3 m height) were identified to species level, with DBH and height (of saplings)
170 recorded. Relative abundance of each species was assessed for trees and saplings combined,
171 based on relative density (stems per hectare), with leaf traits assessed for the species
172 collectively contributing to ≥90 % of total woody plant density, as in de la Riva et al. (2016).
173 Within each sub-plot percentage cover of each understory plant species (including
174 bryophytes) was assessed by eye, tree seedling density recorded and mean foliage height of
175 each species of plant also measured. Epiphytes were not recorded. Leaf traits were also
176 assessed for understory species contributing to approximately ≥90 % of woodland understory
177 cover and were sampled at the main plot level.

178 For each species of tree or sapling selected for leaf trait assessment, three individuals were
179 selected for sampling in each plot. For each individual, three leaves were selected on the basis
180 of: i) height of leaves on trees, all leaves were located on branches accessible from the ground
181 ~1-2 m high; ii) excluding leaves with obvious signs of vertebrate or invertebrate herbivore
182 damage, pathogen damage or necrosis; iii) outer canopy leaves were collected, either sun
183 exposed or least shaded dependant on plot canopy openness (for woodland stand

184 characteristics see Table 2). For each understory species selected for leaf trait assessment
185 three individuals were selected for sampling in each plot. For each individual, three leaves
186 were selected on the basis of: i) foliage height of leaves, with leaves selected from the
187 uppermost foliage in the least shaded part of the plot; ii) avoiding leaf damage as stated above
188 for trees and saplings; iii) for plants with very small or rolled leaves more than three leaves
189 were collected; iv) for bryophytes the top 2 cm of each gametophyte (stem and leaflets) was
190 used as a leaf substitute.

191 Leaves selected for plant trait assessment were collected (while still attached to a length of
192 stem of ~ 2 cm) for trees, saplings and understory plants, wrapped in moist paper and sealed
193 in plastic bags (to avoid dehydration and maximise humidity during temporary storage) as in
194 Perez-Harguindeguy et al. (2013) and placed in a cool box (~ 10 °C). Leaf traits were assessed
195 within 24 hours of leaf collection. Prior to measurement of leaf traits each leaf (including
196 petiole) was cut from its stem and patted dry. One-sided projected leaf area was measured
197 using a Portable Area Meter (LI-3000A, LI-COR) attached to a Belt Conveyer (LI-3050A, LI-
198 COR). Fresh mass and oven-dry mass (60 °C for 72 hours) of each leaf were measured with a
199 4-figure balance. Specific leaf area was calculated by dividing the one-sided area of a fresh
200 leaf by its oven-dry mass (m^2 kg^{-1} or mm^2 mg^{-1}). Leaf dry matter content was calculated by
201 dividing the oven-dry mass (mg) of a leaf by its water-saturated fresh mass (g), expressed as
202 mg g^{-1}. For *Calluna vulgaris*, *Festuca rubra* and bryophyte species projected leaf area was not
203 measured due to their non-flat leaf surface but LDMC was recorded. Each understory plant
204 was allocated one of five growth forms: bryophyte, fern, forb, graminoid (grass, rush and
205 sedge) and shrub.

206 *2.4 Plant tolerance indices*

Shade, drought and water-logging tolerance scores [0 (no tolerance) to 5 (maximal tolerance)] were assigned to tree species using indices developed for European tree species (Niinemets and Valladares, 2006). Shade tolerance indices were largely derived from the Ellenberg indicator for light, drought tolerance indices were based primarily on the inverse of Ellenberg indicator values for moisture and water-logging tolerance (i.e. tolerance of reduced root-zone soil oxygen availability) were based on multiple studies. Ellenberg indicator scores for light [1 (plant in deep shade) to 9 (plant in full light/sun)] and moisture [1 (indicator of extreme dryness) to 9 (submerged plant)] were allocated to understory plants using updated UK values (Hill et al., 1999; Hill et al., 2000) as in Smart et al. (2010) and Kimberley et al. (2014).

2.5 Statistical analyses

All analysis was carried out in R (R core team, 2016). To assess the association between grazing management (grazed *versus* un-grazed) and environmental variables (e.g. soil temperature) linear mixed-effect models were used with plot nested within location to avoid pseudo-replication (i.e. 'random = ~1|Location/Plot'). 'Woodland' is not included as part of the random effect as each pair of woodlands within each location constituted one grazed and one un-grazed woodland, therefore this is accounted for in the grazing effect.

Community-level weighted means (CWM) of trait values were calculated for a set of communities (i.e. plots, n = 3 for each woodland) for: i) trees and saplings combined; ii) trees only; iii) saplings only; and iv) understory plants. For trees and saplings (i, ii and iii) CWM were calculated for 2 plant traits (SLA, LDMC) and 3 tolerance indices (shade, drought and water-logging). For understory plants (iv) CWM were calculated for 3 plant traits (LDMC, mean foliage height, growth form) and 2 Ellenberg indices (light and moisture). For a numeric trait (e.g. SLA), CWM is the mean trait value of all species present in the community (plot),

weighted by their relative abundances (i.e. stem density per plot for trees and saplings, % cover for understory plants), calculated from a species-by-trait(s) matrix. For categorical traits (e.g. growth form), the dominant class is returned as the result (e.g. graminoid or bryophyte). Mean trait values of plant species were used for the calculation of CWM for understory plants (iv) in this study. However, as trees and saplings of the same species (e.g. *Q. petraea*) were often dimorphic (open grown trees *versus* understory saplings), and differed in mean values of plant traits measured in the field (SLA, LDMC) they were considered as separate 'species' for the purpose of calculating CWM for (i) trees and saplings combined. The mean trait (SLA and LDMC) value for each species of tree (ii) or sapling (iii) was used in the species-by-traits matrix. Trees and saplings of the same species were allocated the same score for tolerance indices in the species-by-traits matrix. CWM were calculated using the FD package (Laliberté et al., 2014). Separate CWM values for each of the three plots per woodland were used in a further analysis to assess the association between grazing management and tree, sapling and understory plant traits utilising linear mixed-effects models, nested as described above.

Functional diversity of each woodland community was calculated at the plot level (n = 3 per woodland) for trees and saplings for 2 plant traits (SLA, LDMC) and 3 tolerance indices (shade, drought and water-logging combined). For understory plants, functional diversity was calculated for 3 plant traits (LDMC, mean foliage height, growth form) and 2 Ellenberg indices (light and moisture) combined. Functional diversity was calculated, from the same species-by-traits matrices used in the CWM analysis, using principal coordinates analysis (PCoA) to return PCoA axes, which were then used as 'traits' to compute functional diversity indices, specifically functional dispersion, of each plot using the FD package. Functional dispersion was defined as the mean distance in multi-dimensional trait space of individual species to the centroid of all species, weighted by abundance (Laliberté and Legendre, 2010). For model (i),

254 trees and saplings combined, trees and saplings of the same species were again considered
255 as separate 'species' for the calculation of functional diversity. Functional dispersion was an
256 appropriate index to use in this study as: (a) it is unaffected by species richness, therefore
257 allowing the different trait values of species measured on three individual trees or saplings
258 per plot to be entered into the analysis as different 'species' without artificially inflating the
259 diversity index; (b) it can be computed when traits outnumber species, as occurred for some
260 plots and; (c) it requires only two species to compute functional diversity. In contrast, the
261 suite of three commonly used functional diversity measures, functional richness, evenness
262 and divergence need a minimum of three species per community to be computed.

263

264 **3. Results**

265 *3.1 Environmental and plant community characterisation*

266 The two grazed woodlands were characterised by greater basal area and tree density (total
267 basal area of trees and saplings, and number of tree stems per hectare) than the two un-
268 grazed woodlands, with sapling and tree seedling density greater in the un-grazed woods
269 (Table 2). Diameter size-class distributions showed a greater dominance of the combined tree
270 and sapling populations by the smaller size classes in the two un-grazed than the two grazed
271 woodlands (Appendix, Fig. A2). The two grazed woodlands were dominated by *Q. petraea*
272 trees with some *C. avellana* and *F. excelsior,* while the two un-grazed woodlands were co-
273 dominated by *Q. petraea* and *B. pubescens* trees with saplings of these two species, *S.*
274 *aucuparia* and *I. aquifolium* (Appendix, Fig. A3). Bryophytes, such as *Thuidium tamariscinum*,
275 and the fern *Pteridium aquilinum* occurred in all four woodlands, with graminoids more
276 prevalent in the grazed than the un-grazed woodlands, with cover varying in magnitude with

277 location. Understory shrubs such as *C. vulgaris*, *Vaccinium myrtillus* and *Rubus fruticosus* were
278 only found in un-grazed woodlands (Appendix, Fig. A4). Soil temperature and pH were greater
279 in the grazed than un-grazed woodlands with soil moisture content greater in the un-grazed
280 woodlands (Table 2). Soil bulk density did not differ significantly with grazing.

281 *3.2 CWM of plant traits and tolerance indices*

282 Tree and sapling communities in the main plots had significantly greater LDMC in the grazed
283 than the un-grazed woodlands, with SLA significantly lower in the grazed woodlands (Table
284 3). Tree and sapling communities had significantly higher shade- and drought-tolerance
285 scores but lower water-logging-tolerance scores in the grazed than un-grazed woodlands. The
286 relationship between grazing and LDMC in the woodland plots appeared to be linked primarily
287 to saplings, with differences in the tolerance indices associated mainly with trees (Table 3). In
288 contrast, understory plant trait values did not differ significantly between the grazed and un-
289 grazed woodlands (Table 4). Mean SLA and LDMC of tree, sapling and understory plant species
290 are shown in the Appendix (Fig. A5-A6).

291 *3.3 Functional diversity*

292 Tree and sapling communities had significantly greater functional diversity in the un-grazed
293 than grazed woodlands ($P < 0.01$, Table 5). Understory plant functional diversity did not differ
294 significantly with grazing.

295

296 **4. Discussion**

297 *4.1 Understory community: response-traits*

298 In this study, the understory community did not exhibit clear differences in field-measured
299 plant response traits (LDMC, mean foliage height and growth form) between the grazed and
300 un-grazed Atlantic oak woodlands. We can therefore reject our first hypothesis, based on
301 classic plant-resource models (Coley et al., 1985; Grime, 1977; Westoby, 1998), that response
302 traits associated with grazing tolerance strategies (low LDMC and low mean foliage height)
303 will dominate in grazed understory plant communities. Despite this, there are differences
304 apparent between the woodlands that have not been adequately captured by the plant-trait
305 approach. Whilst bryophytes (high LDMC) occurred in both the grazed and un-grazed study
306 woodlands, the woody shrubs *C. vulgaris*, *V. myrtillus* and *R. fruticosus* (with medium -LDMC
307 values) were only found in the un-grazed woodlands. The understory vegetation of the
308 intensively sheep-grazed woodland was characterised by bryophytes and a mixture of fine
309 (e.g. *F. rubra*) and coarse (e.g. *Deschampsia flexuosa*) grasses (with variable SLA). However,
310 the understory of the feral goat-grazed woodland was dominated by the unpalatable tall
311 tussocky grass species, *Molinia caerulea* (high LDMC). In summary, the understory vegetation
312 of the grazed woodlands was dominated by species exhibiting either grazing tolerance (e.g.
313 small stature, high SLA, low LDMC) or grazing avoidance (e.g. low SLA, high LDMC) strategies,
314 sometimes in combination. A caveat of the plant-trait approach is that community-level plant
315 response trait means for each woodland do not accurately represent these compensatory
316 responses to grazing pressure, especially where antagonistic and synergistic responses cancel
317 each other out.

318 *4.2 Tree and sapling community: response-traits*

319 Whilst the understory plant community is subject to direct contemporary grazing effects, tree
320 and sapling communities are more reflective of the longer-term direct and indirect effects of

grazing on their recruitment and earlier performance. We therefore consider the plant-trait response to grazing of the tree and sapling community separately to the understory community. For the two grazed woodlands in this study, results conformed to the prediction that response traits linked to grazing-avoidance strategies (low SLA and high LDMC) dominate in tree and sapling communities. These results are in line with the findings of Carlucci et al. (2012) but not the grazing tolerance-avoidance frameworks of classic plant-resource models (Coley et al., 1985; Grime, 1977; Westoby, 1998). Whilst potentially useful for characterising plant-response-traits in woodland understory plant communities, these models are not supported by the results of our study, which we suggest indicates that they are not as useful for defining grazing tolerance-avoidance strategies for perennial plants such as trees where true tolerance is rare. Indeed, evidence for grazing-tolerance in woodland ecosystems is sparse and tends to focus on arid woodlands (Meers et al., 2008; Vesk et al., 2004).

An alternative explanation to grazing avoidance or tolerance strategies driving the species composition of grazed woodland communities, is that un-grazed tree and sapling communities contain pioneer trees such as *B. pubescens* as a result of reduced competition, due to the relative lack of mature trees in comparison to the grazed woodlands. These grazing intolerant species exhibit a more 'acquisitive', rapid growth strategy (high SLA, low LDMC) than the species dominant in grazed woodlands, such as *Q. petraea* with a more 'conservative' slow-growth strategy (Díaz et al., 2004). In addition, the two field-measured plant traits (SLA and LDMC) are both leaf traits and do not take into account the variation between tree species in palatability of their bark to grazing livestock, which is important for sapling recruitment. There is evidence that livestock tend to strip the bark of more palatable species, e.g. *Acer pseudoplatanus* and *Castanea sativa*, whereas the bark of others such as *Q. petraea* is more impenetrable to livestock teeth when older (Mayle, 1999). Despite differing in feeding

strategies, both sheep (primarily grazers) and goats (browsers) feed on both whole saplings and tree leaves within reach, particularly when other good quality forage is limited (Pollock et al., 2005). High intensity browsing can reduce growth rates of saplings resulting in trees with a short, wide dwarfed stature and highly branched canopies (Kinnaird, 1974).

4.3 Tree and sapling community: plant tolerance indices

We predicted that shade- and water-logging-tolerance scores would be greater than drought-tolerance scores for both grazed and un-grazed woodlands, due to the high rainfall in the study area. However, results showed that this was not the case, with large differences in scores between the grazed and un-grazed woodlands. Water-logging tolerance scores were greater in the un-grazed than grazed tree and sapling communities reflecting, in part, the low water-logging tolerance score attributed to *Q. petraea* (1.2), dominant in grazed sites, and high score for *B. pubescens* (2.98), found only in un-grazed woodlands. In contrast, drought and shade tolerance scores were greater in grazed woodlands. The characterisation of the grazed woodlands as drought-tolerant communities was largely attributable to their greater dominance by *Q. petraea*, which has a relatively high drought tolerance score (3.02) compared with the species that were more abundant in the un-grazed woodlands, e.g. *B. pubescens* (1.27) and *S. aucuparia* (2.11). Plant species with traits associated with drought avoidance (e.g. leaf shedding or investment in elaborate deep root systems that can reach the water table all year round) can be amongst the best drought survivors, with evidence from tropical dry forests (Poorter and Markesteijn, 2008). The functional traits that describe such drought tolerance or avoidance strategies are at opposite ends of the 'acquisitive-conservative' trait value continuum, e.g. high LDMC, wood density and low SLA in drought tolerant species, low LDMC, wood density and high SLA in drought avoiders. They would

368 nonetheless have similar Ellenberg values and so would not be distinguished by the indices
369 used in this study.

370 *4.4. Tree and sapling community: Functional diversity and resilience*

371 Whilst uncertainty as to the relative tolerance of individual species to future perturbations
372 such as drought or flooding remains, there is now broad consensus that diversity of species,
373 functional diversity in particular, is key to ecosystem resilience (Standish et al., 2014).
374 Therefore, it is likely that communities such as the un-grazed trees and saplings of the present
375 study, which exhibit a wide range of functional diversity for both tolerance indices (e.g. shade,
376 drought and water-logging) and response-plant-traits (e.g. SLA and LDMC), would be more
377 resilient to future perturbations than the grazed plant communities. In addition, the near
378 complete absence of saplings of any species in grazed woodland communities, indicating the
379 indiscriminate impact of grazing on young plants of tree species, with even seedlings of
380 species exhibiting grazer-avoidance traits unable to survive intensive grazing by either sheep
381 or goats. This lack of recruitment leads to even-aged and species-poor grazed woodland
382 communities, low in functional diversity, with potentially compromised resilience to future
383 disturbances. Of particular relevance to this study are climate-related perturbations, i.e. a
384 projected increase in flood and drought intensity, due to the inherent relationship between
385 functional diversity, as defined here, and certain tolerance indices directly linked to water-
386 logging and drought. It is less clear how grazing intensity and functional diversity would relate
387 to non-climatic disturbances such as fragmentation, or afforestation.

388 *4.5. Intraspecific variation or tree/sapling variation?*

389 Increasingly, plant trait-based approaches are addressing the importance of including
390 intraspecific variation in trait values, as using a single trait value to describe a given species

391 can hide functional variation within species, particularly along environmental gradients
392 (Albert et al., 2010). For the present study both *Q. petraea* and *B. pubescens* saplings exhibited
393 greater SLA and lower LDMC than their trees thus allowing for some of the intraspecific
394 difference in traits to be accounted for by entering saplings and trees of the same species into
395 the CWM analysis with different trait values for field-measured traits. There are several
396 reasons why saplings may differ from trees: i) light levels (for photosynthesising leaves) are
397 likely to be lower for saplings than trees, therefore higher SLA and lower LDMC in saplings
398 may increase their carbon gain under these conditions (Spasojevic et al., 2014); ii) leaves from
399 taller trees experience greater drought stress than saplings, as it is drier high up in the canopy.
400 Thicker cell walls and fibres associated with higher LDMC can be important to maintain leaf
401 turgor under lower leaf water potentials in these drier canopy conditions (Kusar et al., 2009;
402 Zimmerman, 1978); iii) exposure of foliage to both livestock herbivores and small mammals
403 such as voles and rabbits is likely to be greater for seedlings and saplings than for larger trees
404 (Palmer et al., 2004), regardless of their growth or defence response-trait strategies, with
405 seedlings and saplings more likely to suffer grazing-induced mortality; and iv) greater LDMC
406 may provide defence against an accumulated invertebrate herbivore population in older trees
407 (Coley, 1983).

408 *4.6 Oak recruitment and grazing*

409 *Q. petraea* saplings were exclusively found in the un-grazed woodlands, indicating a
410 detrimental effect of grazing animals on recruitment of saplings via seedling grazing, as found
411 by Mountford and Peterken (2003) and Vera (2000), though some limited evidence to the
412 contrary was provided by Annighöfer (2015). Coupled with susceptibility to grazing, *Q.*
413 *petraea* is a light-demanding species that can germinate in the shade but needs open

conditions for long-term survival and growth of saplings (Kelly, 2002). In this study *Q. petraea* saplings occurred in semi-open conditions, often close to the thorny shrub *R. fruticosus*, offering the potential of protection from grazing (Kelly, 2002; Vera, 2000). An exclosure experiment, conducted in multiple sites across Europe, found that transplanted *Quercus robur* seedlings grew best in grassland exclosures and on the edge of thorny shrub thickets (Bakker et al., 2004), which may be viewed as an optimal balance between sufficient protection from large herbivores and sufficient light availability.

5. Conclusions

Traditional approaches to woodland conservation and grazing management focus primarily on plant community composition, with sapling recruitment and regeneration of oak (*Quercus* spp.) being a particular concern in the British Isles. More recently, trait-based approaches have been advocated as a basis for conservation management, highlighting the role plant species play in ecosystem function and exploring the relationship between functional diversity and resilience to future perturbations such as flooding or drought. Here, we took a primarily trait-based approach, with plant response-traits, tolerance scores (to shade, drought and water-logging) and functional diversity considered (alongside seedling establishment and sapling recruitment) as potential indicators of ecosystem resilience. In this study, woodlands with a recent history of being un-grazed were characterised by greater seedling establishment, sapling recruitment and tree-level functional diversity than their grazed counterparts, indicating a potential association between management to control grazing and ecosystem resilience in Atlantic oak woodlands.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at xxxx

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643

644 **Table 1** Characteristics of the four study woodlands in north-west Wales, UK.

Location	Ceunant Llennyrch		Nant Gwynant	
Woodland	Llennyrch (L)	Coed Felinrhyd (F)	Hafod y Llan (H)	Llyndy Isaf (I)
Lat/Long (WGS84)	52°55'30.07"N	52°56'06.85"N	53°02'07.49"N	53°01'26.21"N
Elevation (of plots)	~100 m	~ 70 m	~ 70 m	~ 70 m
Grazing category	G	U	G	U
Grazing history	Intensively sheep grazed (80-100 years)	Un-grazed or light sheep grazing in winter only (80-100 years)	Feral goat grazed but sheep excluded (40 years +)	Un-grazed or light sheep grazing in winter only (25 years +)
Condition	Unfavourable	Favourable	Unfavourable	Favourable

645 Condition was reported according to Common Standards Monitoring (CSM) criteria set by the Joint Nature
646 Conservation Committee (JNCC) for Ceunant Llennyrch (Woodland Trust, 2016) and Nant Gwynant (Allen and
647 Brash, 2012; Hearn, 2004; Nouvet et al., 2000). Information on grazing history was also obtained from these
648 references.

649

650 **Table 2** Association of grazing with environmental characteristics of four study woodlands
651 (L, F, H, I) in two locations. Tree (T), sapling (S) and tree seedling summary information are
652 shown for each woodland. Soil variable means are presented for each woodland (n = 3) ±
653 standard error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Grazing
Trees and saplings					
Total basal area (m^2 ha^{-1})	263	138	293	162	↑
T: Stems per hectare (ha^{-1})	1111	889	667	472	↑
S: Stems per hectare (ha^{-1})	0	528	83	1639	↓
Tree seedlings					
Individuals m^{-2}	0.4	1.0	0.1	0.8	↓
Soil					
Temperature (°C)	16.0 ± 0.23	13.6 ± 0.14	14.7 ± 0.10	14.6 ± 0.09	↑ *
Moisture (%)	60 ± 4.20	76 ± 4.70	69 ± 2.97	76 ± 4.20	↓ *
pH (H_20)	4.4 ± 0.07	4.2 ± 0.04	4.4 ± 0.08	4.2 ± 0.04	↑ *
Bulk density (g cm^{-3})	0.26 ± 0.05	0.17 ± 0.05	0.20 ± 0.04	0.13 ± 0.03	*ns*

654 G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing
655 ↑ = larger value, ↓ = smaller value, for G than U woodlands
656 * = $P < 0.05$, *ns* = non-significant
657

Table 3. Association of grazing with tree and sapling community weighted means (CWM) of 2 plant response traits (SLA, LDMC) and 3 plant tolerance indices (shade, drought and water-logging) for four study woodlands (L, F, H, I) from two locations. CWM are presented for trees and saplings combined and separately. Means for each woodland (based on n = 3) ± standard error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Association with grazing
SLA					
Trees and saplings	16.6 ± 1.60	18.4 ±1.04	17.0 ± 1.15	21.2 ± 0.96	↓ *
Trees only	16.6 ± 1.60	16.7 ± 0.50	16.2 ± 1.17	16.9 ± 0.74	*ns*
Saplings only	-	21.7 ± 0.15	23.8 ± 0.0	24.4 ± 0.92	*ns*
LDMC					
Trees and saplings	400 ± 9.8	364 ± 13.5	411 ± 0.6	346 ± 5.1	↑ ***
Trees only	400 ± 9.8	379 ± 9.4	411 ± 0.6	374 ± 13.9	↑ *
Saplings only	-	335 ± 1.7	414 ± 0.0	329 ± 4.2	↑ ***
Shade tolerance					
Trees and saplings	2.77 ± 0.04	2.30 ± 0.10	2.91 ± 0.10	2.65 ± 0.22	↑ *
Trees only	2.77 ± 0.04	2.27 ± 0.14	2.84 ± 0.11	2.20 ± 0.20	↑ **
Saplings only	-	2.14 ± 0.17	3.53 ± 0.00	2.86 ± 0.30	*ns*
Drought tolerance					
Trees and saplings	2.99 ± 0.03	2.00 ± 0.25	3.02 ± 0.00	2.20 ± 0.25	↑ ***
Trees only	2.99 ± 0.03	2.10 ± 0.27	3.02 ± 0.00	1.97 ± 0.40	↑ **
Saplings only	-	1.56 ± 0.15	3.04 ± 0.00	2.25 ± 0.21	↑ *
Water-logging tolerance					
Trees and saplings	1.32 ± 0.12	2.25 ± 0.26	1.31 ± 0.06	1.92 ± 0.22	↓ **
Trees only	1.32 ± 0.12	2.13 ± 0.28	1.26 ± 0.06	2.27 ± 0.41	↓ **
Saplings only	-	2.72 ± 0.14	1.68 ± 0.00	1.82 ± 0.19	*ns*

G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing
SLA = Specific leaf area, LDMC = Leaf dry matter content
↑ = larger value, ↓ = smaller value, for G than U woodlands
*** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, *ns* = non-significant

668 **Table 4**. Association of grazing with understory plant community weighted means (CWM) of
669 3 response traits (LDMC, mean foliage height, growth form) and 2 Ellenberg indices (light
670 and moisture) for four study woodlands (L, F, H, I) from two locations. Dominant growth
671 form is a categorical variable so is shown for each woodland at the plot level. Means for
672 each woodland (based on n = 3) ± standard error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Association with grazing
LDMC	336 ± 26.3	337 ± 11.4	314 ± 18.4	340 ± 7.6	*ns*
Mean foliage height	17.4 ± 6.7	26.6 ± 7.6	34.2 ± 0.8	27.3 ± 2.9	*ns*
Light Ellenberg ind.	5.7 ± 0.12	5.6 ± 0.18	6.2 ± 0.09	6.2 ± 0.16	*ns*
Moisture Ellenberg ind.	5.8 ± 0.15	5.9 ± 0.19	6.5 ± 0.28	6.1 ± 0.46	*ns*
Growth form	Bry/Bry/Fer	Shr/Bry/Fer	Gra/Gra/Gra	Bry/Bry/Gra	-

673 G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing
674 LDMC = Leaf dry matter content, Bry = bryophyte, Fer = fern, Shr = shrub, Gra = graminoid
675 *ns* = non-significant
676

677 **Table 5**. Association of grazing intensity with functional diversity (functional dispersion), for
678 trees and saplings based on 2 response traits (SLA, LDMC) and 3 tolerance indices (shade,
679 drought and water-logging) and for understory plants based on 3 response traits (LDMC,
680 mean foliage height, growth form) and 2 Ellenberg indices (light and moisture) for four
681 woodlands (L, F, H, I) from two locations. Means for each woodland (based on n = 3) ±
682 standard error.

	Ceunant Llennyrch		Nant Gwynant		
	L (G)	F (U)	H (G)	I (U)	Association with grazing
Trees and saplings	0.07 ± 0.07	0.26 ± 0.02	0.07 ± 0.04	0.22 ± 0.04	↓ **
Trees only	0.43 ± 0.43	1.35 ± 0.14	0.28 ± 0.28	0.90 ± 0.28	↓ *
Saplings only	-	0.18 ± 0.09	0.00 ± 0.00	0.16 ± 0.06	↓ **
Understory	0.28 ± 0.02	0.24 ± 0.02	0.28 ± 0.02	0.30 ± 0.00	*ns*

683 G = intensively sheep or feral goat grazed, U = un-grazed or light winter sheep grazing
684 ↓ = smaller value for grazed than un-grazed.
685 ** = $P < 0.01$, * = $P < 0.05$, *ns* = non-significant
686

687